

ROOST SITES OF THE SILVER-HAIRED BAT (*LASIONYCTERIS NOCTIVAGANS*) IN THE BLACK HILLS, SOUTH DAKOTA

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ABSTRACT.—We investigated the roosting ecology of silver-haired bats (*Lasionycteris noctivagans*) in the Black Hills of western South Dakota. Using radiotelemetry, we located 39 roosts, 10 of which were maternity aggregations containing 6 to 55 bats. The roosts were mostly in ponderosa pine (*Pinus ponderosa*) snags that averaged 39 cm diameter at breast height. Solitary bats preferred roosting under loose bark or in crevices in trees, regularly moving among trees. All maternity aggregations were found in tree cavities, primarily those created by woodpeckers. Roost trees were located in patches of forest with relatively high snag densities, about 21 snags/ha. This study suggests that snags play an important role in maintaining silver-haired bat populations in ponderosa pine ecosystems.

Key words: *Lasionycteris noctivagans*, silver-haired bat, roosts, snags.

The silver-haired bat (*Lasionycteris noctivagans*) occurs widely across North America at highly variable densities (Barbour and Davis 1969, Kunz 1982a). Studies conducted in the northwestern United States suggest that silver-haired bats occur more frequently in late-successional forests dominated by trees over 200 yr old than in early series (Perkins and Cross 1988, Thomas 1988). This association is attributed to the presence of high concentrations of standing dead trees, some of which have exfoliating bark, cracks in the wood, and cavities excavated by birds—sites that may be preferred by bats for roosting (Perkins and Cross 1988, Thomas 1988, Campbell et al. in press). Little information on summer roost sites for silver-haired bats is available (Kunz 1982a), particularly in areas that lack abundant stands of late-successional forests. Barclay et al. (1988) searched trees in Manitoba and found silver-haired bats roosting under folds of loose bark during the migration period. Parsons et al. (1986) reported observations of 2 small silver-haired bat maternity colonies in hollow trees in Canada. Likewise, maternity colonies have been found in cavities of both live and dead trees in California (Rainey et al. in press). Despite these records, a clear understanding of silver-haired bat roosts and roost habitat is still lacking.

To better understand the roost requirements of silver-haired bats, we investigated roost selection by the silver-haired bat in the Black

Hills of South Dakota. Although forests in this region have been intensively managed for timber (Boldt and Van Deusen 1974), silver-haired bats are relatively abundant compared to the 9 other bat species present in the region (Mattson 1994). Although Mattson (1994) captured twice as many males as females, pregnant or lactating females were not uncommon. Our goal was to characterize roost selection by silver-haired bats in terms of attributes potentially affected by current forestry practices.

STUDY AREA

Our study area is located in the southern Black Hills of South Dakota near the town of Custer (43°46'N, 103°35'W). Most of the study area is in the Black Hills National Forest and occurs at elevations from 1360 to 1955 m asl. The topography of the area varies from rolling highlands with parklike valleys to narrow, steep canyons with rocky ridge tops. The climate of the Black Hills differs from the surrounding semiarid plains in that it is moister and less subject to temperature extremes. Average maximum temperature at Custer in July is about 23° C, while mean annual precipitation is 457 mm.

The forests of the area are dominated by pure stands of ponderosa pine (*Pinus ponderosa*). Small stands of quaking aspen (*Populus tremuloides*) precede ponderosa pine on disturbed sites. Paper birch (*Betula papyrifera*) grows in small clusters in more mesic sites, whereas

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Rocky Mountain juniper (*Juniperus scopulorum*) grows on dry ridges.

The forests of the Black Hills have been managed for timber production since logging first began in the 1870s. During the past 100 yr, most areas have been cut once, and many have experienced multiple partial cuts (Alexander 1987). In all, nearly 12×10^6 m³ of timber has been removed. Only a few small scattered stands of unharvested forest remain (Boldt and Van Deusen 1974). Although clearcutting was once the primary means of harvest, shelterwood cutting, a method using a series of cuts, is now standard.

We delineated two 10.1×10.1 -km study sites in areas in which we located silver-haired bat roosts. The Jewel Cave Study Site encompasses Jewel Cave National Monument and adjacent areas of the Black Hills National Forest. The Hazelrodt Study Site is located southeast of Custer on national forest land and Custer State Park. Much of the Hazelrodt Study Site burned during a fire in 1990 that covered over 5670 ha.

MATERIALS AND METHODS

Capture and Tracking Techniques

Silver-haired bats were captured using mist nets set above small ponds and streams between 25 June and 4 August 1994. We determined the sex and reproductive condition for all captured bats using external features (Racey 1988). Bats were classified as adult or juvenile based on fusion of the epiphyseal-diaphyseal suture of the finger bones (Anthony 1988).

We attached 0.7-g radio transmitters (model BD-2B, Holohil Systems Ltd., Woodlawn, Ontario) to 4 adult males and 12 adult females. After fur had been trimmed from the bats, transmitters were attached to the area between the shoulder blades using a cyanoacrylate-based glue (Fing'rs, Camarillo, CA). Bats to which transmitters were affixed weighed 11–14 g, so that transmitters represented 5–6.4% of body mass, slightly over the 5% maximum recommended by Aldridge and Brigham (1988). We did not use any other marking technique to identify individuals.

Hand-held, 3-element yagi antennas and portable receivers (model TR-2, Telonics, Mesa, AZ) were used to track bats to roost trees. If we were unable to determine where in the tree the bat was roosting, or whether it was alone or

with others, we returned to the tree before dusk to watch and count bats leaving the site. We attempted to approach the tree quietly to reduce disturbance. We used a bat detector (Bat Box III, Stag Electronics, St. Agnes, England) to listen for echolocation calls. These, along with body size and flight pattern, were used to confirm that bats in a given roost were only silver-haired bats.

Roost Measurements

We located 18 roost trees in the Jewel Cave Study Site and 21 in the Hazelrodt Study Site. When possible, the type of roost (i.e., woodpecker cavity, crevice, loose bark, etc.) was recorded. Each roost tree was classified as being used by either a maternity aggregation or solitary bats. Maternity roosts, located by tracking pregnant and lactating females, always contained 6 or more bats. Solitary roosts contained only a single bat and were located by tracking males or females that did not appear pregnant or lactating or were post-lactating. We categorized the aspect of the roost exit as northeast (0–89°), southeast (90–179°), southwest (180–269°), or northwest (270–359°).

Each roost tree was identified to species and its height and diameter at breast height (dbh) measured. We placed each roost tree into 1 of 7 decay stages; decay stage 1 included live trees with intact bark and branches, whereas decay stage 7 included dead trees beginning to decompose with broken tops and no loose bark (Thomas et al. 1979).

Plot Measurements

Within a 5-m-radius (78-m²) circular plot centered at each roost tree, we measured average tree size, total basal area, and snag density. Trees were defined as standing woody stems >1.5 m in height and >10 cm dbh. We also recorded whether disturbance by fire or logging had taken place in each plot. Disturbance by fire was considered to have occurred if there was any charred woody material in the plot, and disturbance by logging was noted if we observed any saw cuts on woody material in the plot.

To compare characteristics of roost site plots with the surrounding areas, we located four 5-m-radius neighborhood plots for each roost plot and recorded the same information as for roost plots. We located the center of the neighborhood plots by pacing 100 m from the roost

tree in each of the cardinal directions (north, south, east, west) and then pacing an additional 30 m in a randomly selected direction.

We measured elevation and distance to the nearest source of water for each roost tree using topographic maps (7.5 minute series, USGS, Denver, CO). For comparison, we randomly located a point in the Jewel Cave Study Site or Hazelrodt Study Site for each roost tree found in that site. To examine roost site selection on a larger scale, we calculated the number of snags in all neighborhood plots to estimate snag density for the study site generally. This estimation was made by dividing the total number of snags in the 156 neighborhood plots by their total area. The fire in the Hazelrodt Study Site inflated snag densities in this area. To remove the influence of fire, we calculated snag densities within the study sites by removing the 77 neighborhood plots that had been disturbed by fire.

Analysis

Chi-square tests for goodness-of-fit (Jelinski 1991) were used to compare observed with expected roost aspects and tree decay stages by roost type (maternity vs. solitary). For the latter test, because of small sample size, we pooled the roost trees into 3 decay stage categories: stage 1–3, stage 4, and stage 5–7.

To compare continuous attributes between roost plots and neighborhood plots, we subtracted attribute means for the 4 neighborhood plots from corresponding means for the roost plots. So, each roost plot was compared only to its 4 neighborhood plots. We tested the null hypotheses that the mean differences did not differ from 0 using paired *t* tests. Chi-square tests for homogeneity (Jelinski 1991) were used to compare observed with expected disturbances at roost plots. Expected disturbances were based on the proportion of neighborhood plots that had burned or been logged. We used 2-sample *t* tests to compare the means for elevation and distance to nearest water for roost sites and random sites. To avoid type 1 errors that may result from using a number of inferential statistical tests with the same predictor variable, we arbitrarily set $\alpha = 0.025$.

RESULTS

Roost Attributes

We radio-tracked 16 bats for a mean of 8 d (range: 1–20) and located 39 roosts, all of

which occurred in trees. Nine adult females were tracked to 10 trees that were used by maternity aggregations averaging 22.2 ± 4.9 (s_x) individuals (range: 6–55). Three other females and 4 adult males were tracked to 25 roost trees, none of which were used by maternity aggregations. Three of the females that originally used maternity aggregations were later followed to 4 trees where they roosted alone. Maternity roosts were found exclusively in tree cavities, primarily those created by woodpeckers (Picidae). Cavity openings were 7.5–10 cm in diameter. Solitary bats roosted under loose bark ($n = 15$), in a tree crack or crevice ($n = 5$), or in a woodpecker cavity ($n = 1$). We could not determine the specific roost location for 8 trees. These trees were placed in the solitary category because bats tracked to these 8 trees were always observed roosting alone at other trees. Maternity roosts were 10.2 ± 1.5 m (range: 3.1–13.8) aboveground. The height of measured solitary roosts averaged 3.4 ± 0.5 m (range: 0.9–8.9). Cavity openings of maternity roosts and solitary bat roosts were found more frequently on the south side of tree boles over other aspects ($\chi^2 = 15.8$, d.f. = 3, $P = 0.001$).

Of 39 roost trees, 38 (97%) were ponderosa pine and 1 (3%) was aspen. Of 508 trees on neighborhood plots, 483 (95%) were ponderosa pine and 25 (5%) were other species: aspen, juniper, and paper birch. The 10 trees used by maternity aggregations of silver-haired bats ranged from decay stage 2 to 7 (median = 5). The 29 trees used by solitary bats varied from tree decay stage 3 to 7 (median = 4). Trees in neighborhood plots ranged from decay stage 1 to 7 (median = 1). Bats in maternity aggregations selected roost trees in significantly different decay stages than solitary roosting bats ($\chi^2 = 10.2$, d.f. = 2, $P = 0.0062$; Fig. 1). Roost trees averaged 14.2 ± 0.9 m (range: 3.7–24.1) in total height, and 39 ± 2 cm dbh (range: 13–63). They averaged 17 ± 2 cm larger in dbh than neighborhood trees. The 10 maternity roost trees averaged 44 ± 4 cm dbh (range: 29–62), 24 ± 4 cm larger than neighborhood trees. The 29 solitary roost trees averaged 37 ± 2 cm dbh (range: 12–55), 15 ± 3 cm larger than neighborhood trees. Maternity and solitary roost trees did not differ in diameter ($t = 1.64$, $P = 0.12$).

The 9 bats found in maternity aggregations returned to the same roost tree for a mean of 8 d (range: 1–21). We tracked 1 bat from a tree containing a maternity aggregation of 55 bats

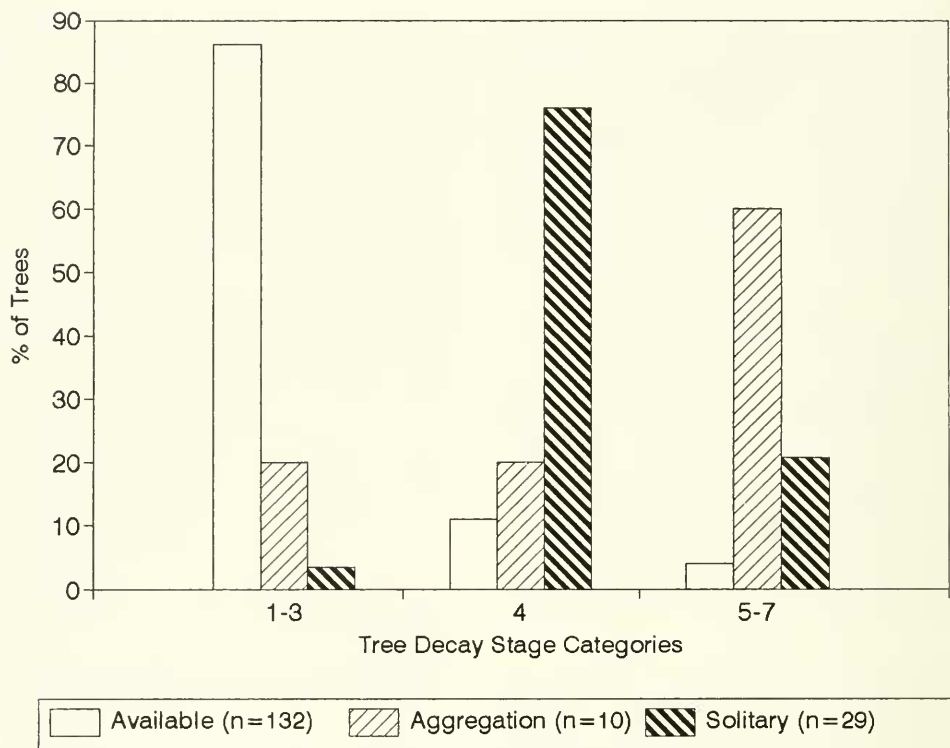


Fig. 1. Percentages of trees in each tree decay stage category used by maternity aggregations and solitary roosting silver-haired bats, and available trees in the Black Hills, South Dakota, June–August 1994.

to a 2nd tree with a maternity aggregation of 44 bats about 440 m away. The following evening no bats were observed exiting from the 1st roost tree, but it is not clear how many bats from the 1st roost tree moved to the 2nd tree with the bat we were tracking.

We tracked 10 bats that used solitary roosts to a mean of 3 solitary roost trees (range: 1–6). For the most part, these bats switched trees daily. However, on 5 occasions solitary bats used the same tree on consecutive days. Three of the 7 solitary roosting bats that we followed to multiple trees returned at least once to trees they had used several days before. Solitary roosting bats traveled a mean of 405 ± 93.7 m ($n = 13$) between successive roost trees. Radio-tracked bats traveled a mean of 2060 ± 440 m ($n = 12$) from the capture point to their first roost tree, significantly farther ($t = 3.67$, $P = 0.004$) than the distance between successive roost trees.

Live and dead trees on roost plots were 6.5 ± 1.7 cm larger in dbh on average than those on neighborhood plots ($t = 3.77$, $P = 0.0006$). Roost plots also had basal areas of both live and dead standing trees that were 14.07 ± 3.46 cm²/m² greater ($t = 4.06$, $P = 0.0002$) than neighborhood plots. Neither fire disturbance ($\chi^2 = 0.005$, d.f. = 1, $P = 0.94$) nor logging disturbance ($\chi^2 = 2.72$, d.f. = 1, $P = 0.099$) differed between roost and neighborhood plots. Maternity and solitary plots did not differ in the attributes studied (Table 1). Roost trees tended to be located higher in elevation than random points ($t = 1.67$, $P = 0.10$). Roost sites were significantly farther from water than random points ($t = 2.78$, $P = 0.007$).

Using all 156 neighborhood plots, we calculated snag density for the area to be 117 snags/ha. After removing 77 neighborhood plots that were disturbed by fire, we recalculated snag densities to be 21 snags/ha.

Plot Attributes

Roost plots had 1.7 ± 0.6 more live trees ($t = 3.09$, $P = 0.004$) than neighborhood plots.

DISCUSSION

Roosts used by maternity aggregations differed from those used by solitary silver-haired

TABLE 1. Comparison between solitary and maternity roost plot attributes in the Black Hills, South Dakota, June–August 1994.

Attribute	Solitary (<i>n</i> = 29)	Maternity (<i>n</i> = 10)	<i>T</i>	<i>P</i> value
Live trees (no./plot)	4.5 ± 0.6	5.2 ± 0.7	0.72	0.47
Snags (no./plot)	2.1 ± 0.5	2.2 ± 0.5	0.15	0.88
Mean tree dbh (cm)	26.7 ± 3.2	27.5 ± 1.9	0.22	0.83
Total basal area (cm ² /m ²)	17.8 ± 1.3	25.3 ± 4.7	1.54	0.13

bats. Maternity aggregations always used a hollow cavity within a tree bole. Usually these cavities were created by woodpeckers, likely hairy woodpeckers (*Picoides villosus*) or black-backed woodpeckers (*P. arcticus*), based on the size of the openings (Terres 1980). Although rare in the Black Hills (Black Hills National Forest 1989), Lewis' woodpeckers (*Melanerpes lewis*), northern flickers (*Colaptes auratus*), or three-toed woodpeckers (*Picoides tridactylus*) may have excavated some of the cavities. Solitary roosts were located under loose bark or in a natural crack or crevice in the tree bole. Only once did a solitary bat use a woodpecker cavity. Although silver-haired bats are cryptically colored, they were never observed roosting openly on a tree trunk or limb, or in foliage. This behavior differs from other cryptically colored, tree-roosting bats (e.g., *Lasius* spp.), which tend to roost among tree foliage (Shump and Shump 1982a, 1982b). Roosts required by maternity aggregations may limit silver-haired bat abundance; clearly trees with cavities are less available than are those without. Reproductive females seem to require roosts that provide a relatively enclosed and unexposed space for protecting young from predators or maintaining the necessary thermal environment.

Cavity openings of maternity roosts and solitary bat roosts occurred more frequently than expected on the south side of tree boles. We hypothesize that these roosts are warmer than sites facing north because of insolation and that these differences result in energetic savings, providing more energy for growth and development (McNab 1982). Reller (1972) has shown that several species of woodpeckers orient their nest cavity openings southwesterly for warming by the sun and/or ventilation by the wind. However, it is unclear whether bat use

of cavities with south-facing entrances reflects the selections of bats or woodpeckers.

Silver-haired bats roosted exclusively in trees during the summer. Although all but one of the roosts were located in ponderosa pine trees, the dominance of ponderosa pine in our study area prevented us from testing for tree species preference. The wide geographic distribution of silver-haired bats relative to that of ponderosa pine and the use by silver-haired bats of both coniferous and deciduous roost trees in other parts of their range (Novakowski 1956, Parsons et al. 1986, Barclay et al. 1988, Campbell et al. in press, Rainey et al. in press) suggest that these bats select for the structure of the roost itself rather than for a particular tree species. As for other tree-roosting bats (Tidemann and Flavel 1987), it is unlikely that tree species is important to silver-haired bats except that at the local level 1 species may tend to have preferred attributes.

Roost trees were standing, dead, and larger than average in diameter. The single living tree selected as a roost was dying (stage 2) and missing its top; it also had many dead limbs and several woodpecker holes high in the bole. There was an observed difference in tree decay stage between roost trees used by maternity aggregations and solitary bats. Solitary roosting bats frequently used trees in decay stage 4, which are characterized by the presence of loose bark. Alternatively, maternity roosts tended to be found in older, more decomposed trees (decay stages 5–7), trees that are more commonly used by excavating woodpeckers (Thomas et al. 1979). Although the importance of snags as roost sites in other forest types remains in question, large snags appear to be important resources for silver-haired bats in ponderosa pine forests.

Clearly, solitary roosting silver-haired bats switch roosts regularly. This lack of fidelity may be related to the abundant nature of potential roosts (Brigham 1991) or a predator-avoidance strategy (Kunz 1982b). Because they will return to roost trees used several days previously and these roosts are often close together, solitary bats may use a series of trees in the same area and thus maintain a level of site familiarity. Conversely, maternity aggregations tend to remain in the same roosts for longer periods. This may be related to the less abundant nature of tree cavities and the importance of retaining roosts that are suitable for raising offspring. At least some of the maternity aggregations appear to switch roosts during the reproductive period. The reason for this is not clear, although it may involve predator or ectoparasite avoidance (Lewis 1995).

We expected bats to select roosts relatively close to water bodies, minimizing energetic costs of moving between roosting areas and areas potentially used for drinking and foraging. Although trees were abundant in the study sites, bats traveled an average of >2 km from point of capture to their 1st roost tree, and significantly farther from water than expected randomly. This seems to support other available evidence for insectivorous bats in that roost site location is not strongly influenced by commuting costs (Fenton et al. 1985, Brigham 1991). Roost sites located farther from water than random points appear puzzling but may represent the large number of roost trees located along hill or ridge tops, sites with potentially higher snag densities.

Silver-haired bat roost trees were found at sites that differed from nearby areas in a number of attributes. Roost plots differed in having more, large trees and hence a higher total basal area than surrounding plots. Roost trees located in areas that are ideal for tree growth or are logged infrequently might explain why the roost plots have more, larger trees.

Undoubtedly, snags are important in providing roost sites for silver-haired bats in the Black Hills. As suitable roosts are critical resources for bat survival (Kunz 1982b), snag availability likely influences the distribution and abundance of this species. Forest stands containing silver-haired bat roosts had snag densities of 21 snags/ha, a value much higher than current management objectives. These densities were even higher in the Hazelrodt

Study Site, an area with a large number of fire-killed trees. How fire suppression and logging practices have affected the number of snags in the Black Hills remains unclear; however, early photographs suggest that many forested areas were more open with many standing dead trees (Knight 1994). Because snags are used for nests or roosts by a large number of vertebrate species (Thomas et al. 1979), reduced snag densities may increase interspecific competition. We hypothesize that forest management practices that reduce snag densities will lead to declines in local silver-haired bat populations.

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